

The natural history of reproduction in *Solanum* and *Lycianthes* (Solanaceae) in a subtropical moist forest

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SYNOPSIS. The phenology and pollination of seven understory species of buzz-pollinated Solanaceae (*Solanum erythrorichum*, *S. lanceifolium*, *S. rudepannum*, *S. cordovense*, *S. nudum*, *Lycianthes hypoleuca* and *L. gorgonea*) were investigated at the end of the dry season in the subtropical moist forest at the Las Cuevas Research Station, Chiquibul Forest Reserve, Cayo District, western Belize. Three phenological phenomena were tracked: the opening and closing of flowers, flower production and fruit production. The large short-lived white flowers of *S. lanceifolium*, *S. rudepannum*, *Lycianthes hypoleuca* and *L. gorgonea* opened around sunrise and closed at sunset. The purple flowers of *S. erythrorichum* and the small white flowers of *S. nudum* and *S. cordovense* opened more or less randomly. All seven study species flowered at least once during the months of May, June and July; there was substantial overlap in the flowering of some species. Four species, *S. rudepannum*, *S. cordovense*, *S. lanceifolium* and *S. erythrorichum*, developed mature fruit during the monitoring period while the remaining species possessed immature fruit at the termination of the study. Thus, it appeared that these seven solanaceous species would provide a fairly constant supply of mature fruit during the rainy season. During observations of pollinators, 17 different bees in the families Colletidae, Halictidae and Apidae were found to visit the buzz-pollinated flowers of *Solanum* and *Lycianthes*. Analysis of the pollen loads revealed that bees were highly constant to Solanaceae although it was not possible to determine their constancy to particular species. Very few visits were observed to *S. cordovense* and *L. gorgonea*.

INTRODUCTION

The Solanaceae is an economically important, cosmopolitan family with over 2500 species in some 90 genera. The family has members occurring in all habitats, and their habit ranges from canopy trees to minute ephemeral herbs. Flowers in the family Solanaceae exhibit a wide array of forms (Knapp, 2002), and are pollinated by a similarly

wide variety of organisms, including bees, hummingbirds and bats (Cocucci, 1999). In Mesoamerica, the family is an important component of the forest understory in a variety of habitats, and in Belize, it is the eleventh most diverse vascular plant family overall (Balick et al., 2000).

Solanum L. and *Lycianthes* (Dunal) Hassl. are the two largest genera in the family (D'Arcy, 1991). *Solanum* comprises 1500 or more species, 800–900 of which occur in the New World (D'Arcy,

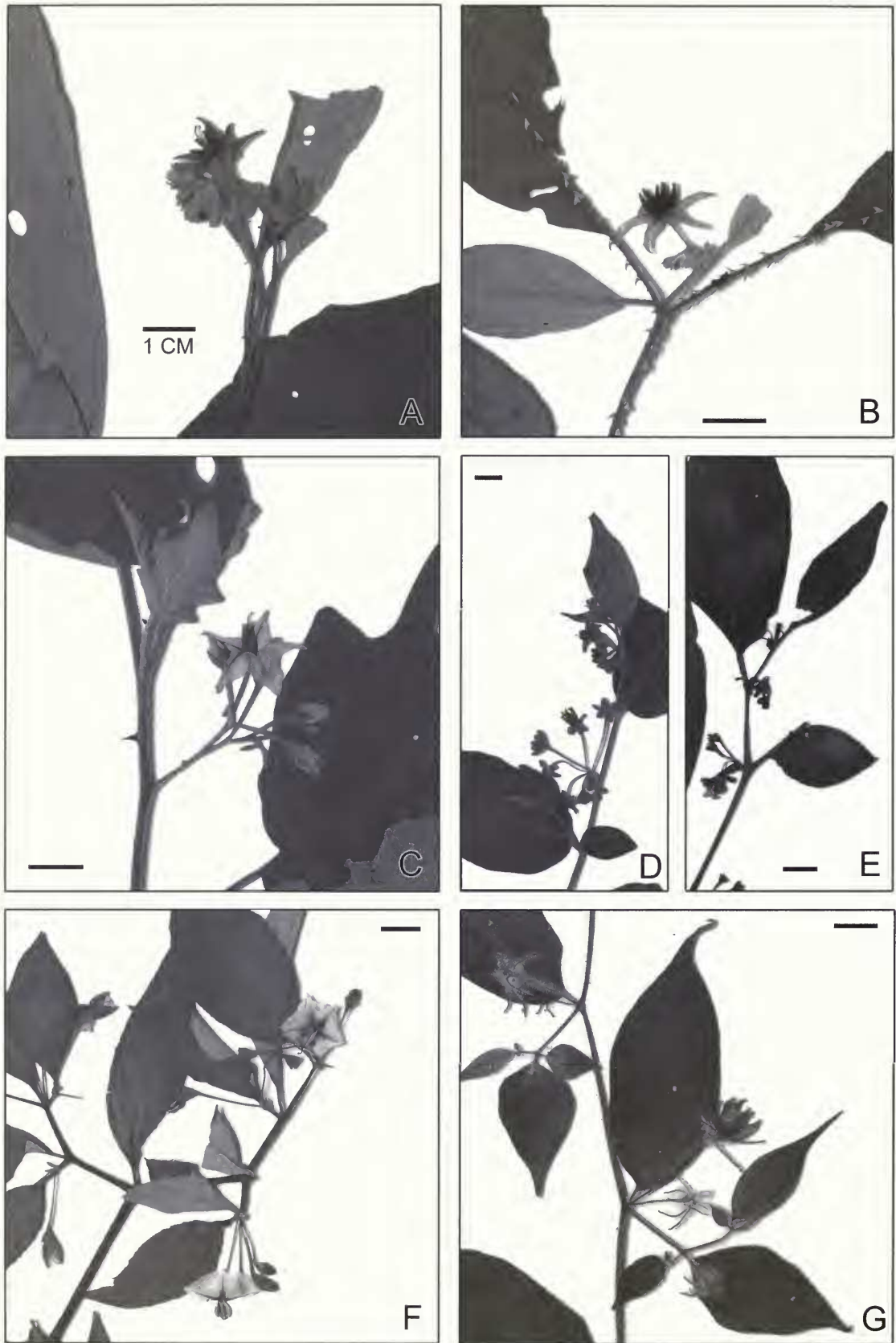


Fig. 1 Study species of Solanaceae at LCRS. Photographs taken from vouchers cited in the text. A. *Solanum erythrotrichum*, B. *S. lanceifolium*, C. *S. rudepannum*, D. *S. cordovense*, E. *S. nudum*, F. *Lycianthes hypoleuca*, G. *L. gorgonea*. Scale bar = 1 cm.

1991; Nee, 1999). *Lycianthes* contains approximately 200 species distributed in both tropical America and Asia (D'Arcy, 1973, 1979; Symon, 1985), and despite being superficially similar to *Solanum* (see below), it is closely related to the genus *Capsicum* L. (Olmstead et al., 1999). Approximately ten species of *Lycianthes* and 30 species of *Solanum* occur in Belize (Balick et al., 2000; Knapp et al., in press).

Although phylogenetically distant, members of *Solanum* and *Lycianthes* share similar, convergent, floral morphology. The flowers possess a five-parted gamopetalous corolla. The five equal stamens are fused to the corolla tube, and the bright yellow tubular anthers form a cone around the style (typical 'solanoid' flowers, Endress, 1994; Fig. 1). The flowers of *Solanum* and *Lycianthes* are buzz-pollinated (Buchmann, 1983; Nevers, 1986; Lester et al., 1999). When buzzing a flower, an insect grasps the cone of tubular anthers with the front pairs of legs, wraps the abdomen around the apical pores of the anthers, and vibrates the anthers by rapidly contracting the indirect flight muscles (Michener, 1962; Buchmann & Hurley, 1978). This audible action causes pollen to burst out of the anther and land onto the venter of the insect. As the flowers of these *Solanum* and *Lycianthes* species offer no nectar and little scent, pollen is the only reward available to their pollinators (Symon, 1979; D'Arcy et al., 1990; pers. obs.). Although the mechanism of buzz pollination in Solanaceae has been well characterized (Michener, 1962; Buchmann, 1983), detailed studies which identify both the buzz-pollinated plant species and their pollinators are few (but see Linsley & Cazier, 1963; Anderson & Symon, 1988).

Here we examine the phenological patterns and pollination biology of seven sympatric buzz-pollinated species of *Solanum* and *Lycianthes* in the Chiquibul forest of western Belize. In studying their phenology, we tracked the daily opening and closing of flowers as well as the seasonal timing of flower and fruit production. Characterizing these daily and seasonal floral events in turn set the stage for investigations of pollination biology. In undertaking this study, we seek to expand our knowledge of Solanaceae in Belize, their natural history and range of pollinators.

METHODS

Study site

The Chiquibul Forest Reserve, Cayo District, western Belize, is nested completely within the Chiquibul National Park (Fig. 2). The vegetation comprises deciduous semi-evergreen and deciduous seasonal forest with stands of Caribbean pine to the north (Wright et al., 1959). The Macal River roughly divides the Caribbean pine forest to the north from the broad-leaved tropical forest of the Chiquibul to the south. Las Cuevas belongs to the subtropical moist life zone (Holdridge et al., 1971). While largely protected, some selective logging of commercial species such as mahogany (*Swietenia macrophylla*) and cedar (*Cedrela odorata*) is carried out in the Chiquibul on a >40 year rotational basis. The area has also suffered hurricane damage in the past (most recently from Hurricane Hattie in 1961), and the forest is a mosaic of different successional stages.

Our field studies were carried out at the Las Cuevas Research Station (LCRS) (16°44' N, 88°59' E; altitude 550–600 m; Fig. 2) operated jointly by the Forest Department of the Government of Belize and The Natural History Museum, London. Las Cuevas is situated in the centre of the Chiquibul Forest Reserve on the north-western side of the Maya Mountains, and has an annual rainfall of c. 1500 mm. The dry season at Las Cuevas runs from December to May, while the rainy season begins in mid to late June and ends in

January. This study began on 27 May 2000 and continued until 23 July 2000, thus covering the transition from the dry season to the wet season. The flowering of understory herbs including *Solanum* is known to peak during this transition period in Costa Rica and in Panama (Croft, 1969, 1975; Opler et al., 1980; Knapp, 1986), and in cerrado habitats in Brazil (Oliviera & Gibbs, 2000). Therefore, June and July were expected to be ideal months in which to study the reproductive biology of the understory Solanaceae in Belize. Though the study was conducted primarily along a trail to Monkey Tail River, pollinator behaviour was also studied at an observation tower located 1 km northwest of the station.

Taxa studied

The habit, flowers and fruit of the seven species studied at Las Cuevas are briefly described below. The *Solanum* species are listed in their respective infrageneric taxon (sensu Nee, 1999). The infrageneric classification of *Lycianthes* is not well understood, so this information was not included in the descriptions below.

- *Solanum erythrotrichum* Fernald (Subgenus *Leptostemonum*) – An erect spiny shrub, with purple flowers (2 cm in diameter), tapering anthers and globose, slightly hairy green hard fruit, around 1.5 cm in diameter. It is commonly found in partly shaded disturbed areas and tree falls. (Voucher: S.D. Smith 008, BRH, BM). Fig. 1A
- *S. lanceifolium* Jacq. (Subgenus *Leptostemonum*) – A herbaceous weedy vine with short recurved spines. Its flowers are white, up to 2 cm in diameter with tapering anthers, and the small round fruit are 1 cm in diameter and bright red at maturity. It is found in thickets and in the canopies of small to medium trees. (Voucher: S.D. Smith 034, BRH, BM). Fig. 1B
- *S. rudepannum* Dunal (Subgenus *Leptostemonum*) – An erect spiny shrub, which produces large white flowers up to 2.75 cm in diameter and hard round berries which are about 2 cm in diameter and green at maturity. It prefers clearings such as road verges and fields. (Voucher: S.D. Smith 013, 037, BRH, BM). Fig. 1C
- *S. cordovense* Sessé & Moç. (Subgenus *Solanum*) – A clambering woody shrub with small white flowers (1 cm in diameter). The fruit is a globose juicy black berry, 1–1.25 cm in diameter. It is common along partly shady trails or in thickets. (Voucher: S.D. Smith 002, BRH, BM). Fig. 1D
- *S. nudum* Dunal (Subgenus *Solanum*) – A ubiquitous, entirely glabrous shrub with small white flowers similar to those of *S. cordovense*. Its fruit are yellowish-green berries of 1 cm in diameter. It is abundant in sunny areas along trails and roads. (Voucher: S.D. Smith 038, BRH, BM). Fig. 1E
- *Lycianthes hypoleuca* Standl. – A vigorous climbing shrub with large rotate white flowers (1.8–2 cm in diameter) and round red fruits just under 1 cm in diameter. It is found occasionally in small forest gaps or on hillsides, either in part-shade or full sun. (Voucher: S.D. Smith 026, BRH, BM). Fig. 1F
- *L. gorgonea* Bitter – A delicate scandent shrub with flowers similar to those of *L. hypoleuca*. Its fruit are slightly ovate, red berries of about 1 cm in diameter. It is quite infrequent, occurring only in the shady understory. (Voucher: S.D. Smith 012, BRH, BM). Fig. 1G

Floral phenology

Information was systematically collected on the time of opening, the time of closing and the extent to which the corollas were open (e.g., partly open to fully open with petals reflexed). These data were used to characterize the movements of the corolla and the longevity of the

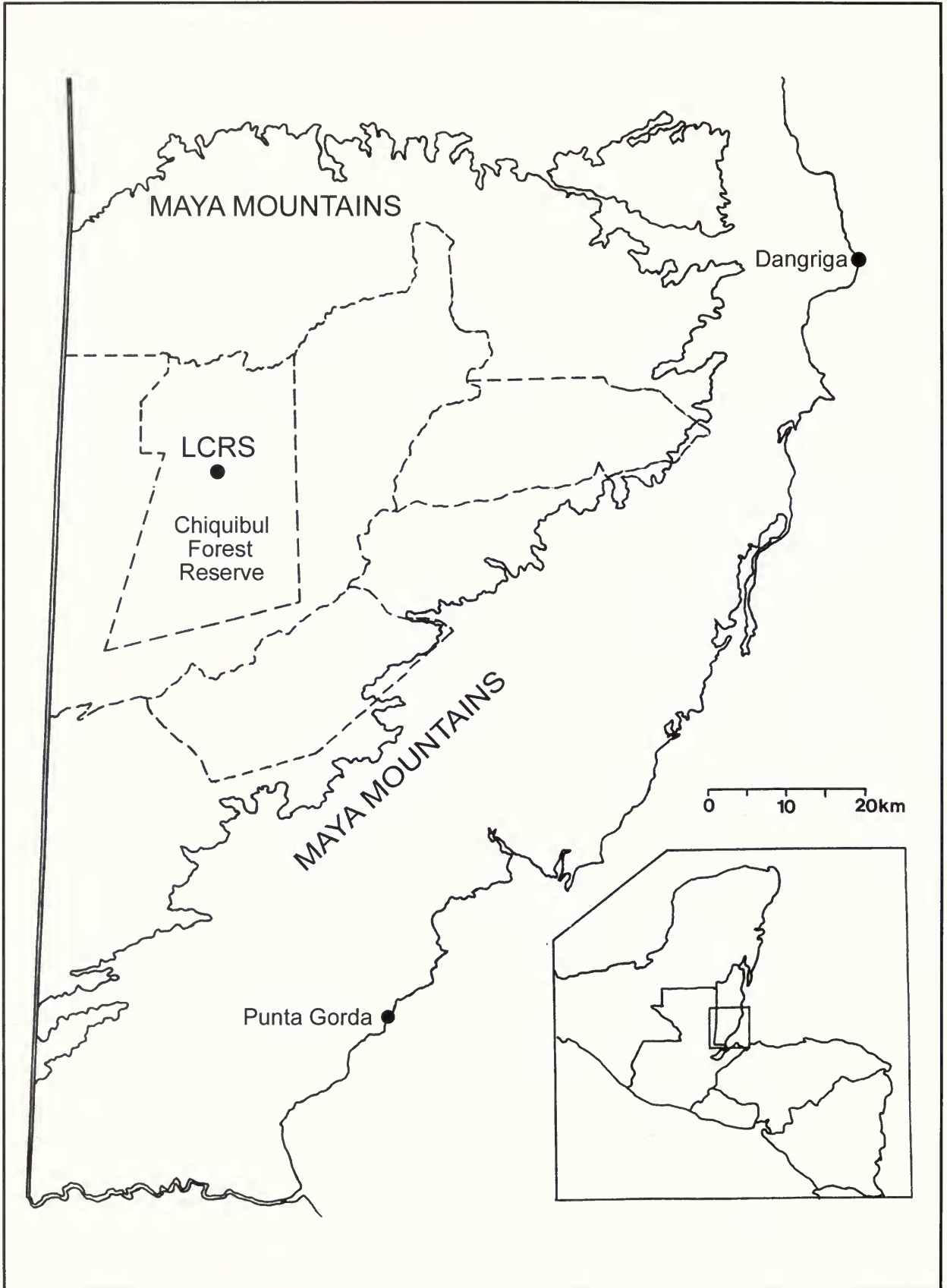


Fig. 2 Map of southern Belize (Belize shown in inset) showing position of Chiquibul Forest Reserve and the Las Cuevas Research Station (filled circle).

flowers. One mature individual was selected from each of the study species, and up to 25 flowers per individual were tagged and monitored for their entire lifespan. At the beginning of the study, the flowers were checked every four hours. Once it was determined whether the flowers of a given species close at night or not, flowers were checked only from 0500 hours to 2100 hours for the remainder of the study. The position at 0100 hours was interpolated from observations at 2100 hours and 0500 hours. For example, if the corolla was 50% open at 2100 hours and was 100% open at 0500 hours, its position at 0100 hours was recorded as 75% open. At Las Cuevas, the sun rises around 0500 hours and sets at 1845 hours. The position of the petals was recorded as follows: 0 = unopened bud (beginning) or flower dead (end); 0.1=closed but petals not appressed as in the bud; 0.25=flower 25% open; 0.50=flower half-open; 0.75=flower 75% open; 1.0=flower open with petals perpendicular to the pedicel; 1.25=flowers with petals reflexed. After the flower bloomed, 0.1 indicated that the flower had closed but remained attached whereas 0 indicated that the flower had fallen off. A flower was considered open to visitors when it was 40% open; below that level the aperture was too small for the bees to access the reproductive organs (pers. obs.).

Flower and fruit production

All mature individuals (up to a maximum of 25) of the seven study species present in the first two kilometers of the trail to Monkey Tail River were tagged, and (starting June 1) every three days, the number of inflorescences, flowers and fruit was recorded. An inflorescence was counted from the moment it was visible at the tip of the branch to the abscission of its last flower. *Lycianthes gorgonea* and *L. hypoleuca* were not included in the counts of inflorescences because the flowers occurred singly. A flower was counted if its petals were open sufficiently so that the cone of anthers could be easily seen. Fruit were only counted when the ovary had doubled in size, i.e., once they were so large that it was clear that they would not be aborted. Approximate canopy cover was also recorded for each individual in the study in order to make a preliminary assessment of its effect on these species. The percent canopy cover above each individual was estimated visually and recorded in one of the following five categories: 0% cover, 25% cover, 50% cover, 75% cover and 100% cover.

Flower visitors

Observations were taken from 0400 hours to 1900 hours and sporadically throughout the night. Flower visitor activity was most intense between sunrise and noon, so most observations took place between 0500 hours and 1200 hours. Observations included time of visit, number of flowers visited, length of visit and activities on the flowers. Each study species was observed for 18 to 20 hours or more. Every different visitor was collected using a sweep net and transferred directly into an eppendorf tube containing 1 ml isopropanol. Bees too large to fit into a tube were immediately washed in isopropanol to remove pollen, and this pollen sample was kept for pollen analysis (see below). When possible, several specimens of each visiting species were captured, so that later pollen load analysis could give some indication of the overall constancy of the species. Chris O'Toole (Oxford University) identified each bee to genus level and to species when possible.

Pollen load analysis

To remove pollen, each bee was transferred from its eppendorf tube to a 12 ml glass tube. The eppendorf tube was rinsed out with an additional one ml of isopropanol, which was added to the glass tube.

Each bee was then shaken vigorously for 30 seconds to free the pollen from the body. The body was visually checked afterwards to assure that the pollen had been removed, and washed further if necessary. The tubes containing the pollen suspended in isopropanol were centrifuged at 5000 × g for five minutes to pellet the pollen. The isopropanol was poured off and the tubes inverted on a paper towel to drain. Then, 0.3 ml melted glycerol jelly was added to the pellet and stirred. One drop of this mixture was poured onto a glass slide and topped with a slide cover. Three hundred pollen grains were counted on each slide, and the percentage of solanaceous pollen calculated from this count. Solanaceous pollen was distinguishable from other pollen grains because it is small, smooth and tricolporate. It was not possible to distinguish between the study species with the light microscope. Density of pollen grains was estimated at 40x magnification and was coded as follows: 1=one pollen grain per view or less; 2=1 to 5 pollen grains per view; 3=5 to 10 pollen grains per view; 4=10 to 20 pollen grains per view; 5=greater than 20 pollen grains per view.

RESULTS

Floral phenology

Based on the data collected, the seven species could be divided into two basic groups: those whose flowers opened at sunrise and those whose flowers opened throughout the day and night. The flowers of *Solanum lanceifolium*, *S. rudepannum*, *L. hypoleuca* and *L. gorgonea* opened around 0500 hours, sunrise at Las Cuevas, and closed between 1700 and 2100 hours (Fig. 3B, C, F, G). The flowers of *S. cordovense* and *S. nudum* opened more or less randomly throughout the day and night and remained open through the night, creating the potential for nocturnal pollination (Fig. 3D, E). The corolla of some *S. cordovense* flowers closed partially during the night although never sufficiently to exclude pollinators entirely. *Solanum erythrorichum* (Fig. 3A) was an intermediate between these two basic groups as its flowers only opened between 0600 and 1300 hours (instead of right around sunrise) and closed at night.

Great variation in the synchrony of flower movements was observed among the seven species. Fig. 3 shows the average position of a corolla of a given species throughout the day. For each data point, standard deviation was calculated to show the variation in corolla position between flowers of the same species. Several species show extreme asynchrony in opening and closing, such as *Solanum cordovense* and *S. nudum*, both of which had long-lived (Fig. 3D, E), small, white flowers less than 1 cm in diameter. This is consistent with the observation that their flowers open randomly throughout the day and night. The large showy white flowers of *S. rudepannum*, *Lycianthes hypoleuca* and *L. gorgonea*, ranging from 1.75 to 2 cm in diameter, opened much more uniformly, particularly on their first day (Fig. 3C, F, G). Flowers of the latter normally opened for one day only (Fig. 3C, F, G), with occasional flowers opening on a second day (perhaps due to lack of pollination).

The flowers of *S. lanceifolium* usually opened to some extent for a second day although they were rarely visited by the bees, which could apparently discern the older flowers (Fig. 3B) (see below). The petals of *S. nudum* remained reflexed for only the first 4 to 12 hours, then the flowers slowly closed over the next day. The petals of *S. cordovense* flowers were reflexed for fewer consecutive hours although they were capable of returning to the reflexed position for several days in a row. This suggests that they continued to be receptive to pollinators for several days after opening or that the reflexed petals act as a pollinator attractant.

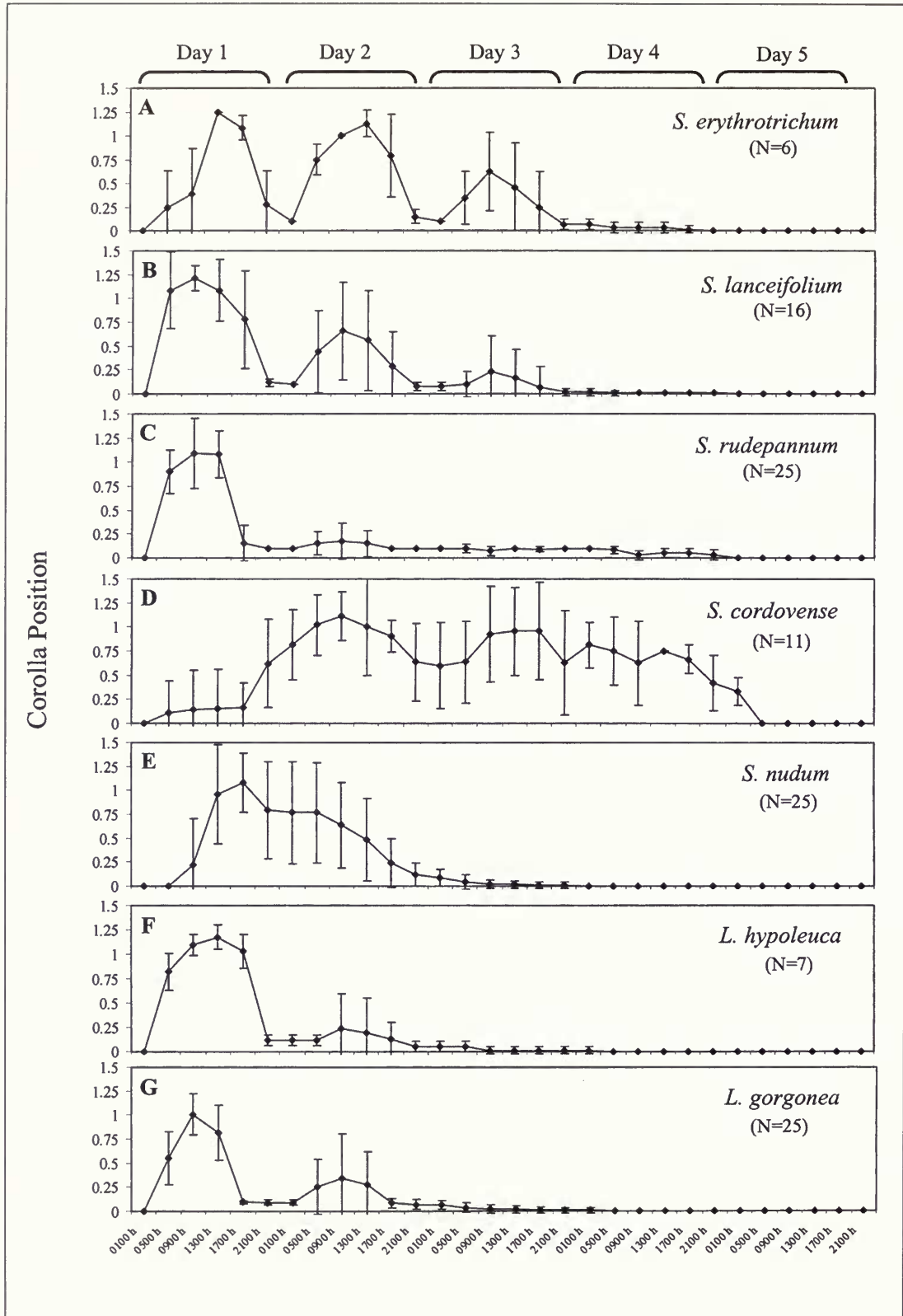


Fig. 3 Corolla movements. Data from up to 25 flowers was combined to produce the graphs. The position of the petals on each flower monitored was recorded every 4 hours using the following scale: 0 = unopened bud (beginning) or flower dead (end); 0.1 = closed but petals not appressed as in the bud; 0.25 = corolla 25% open; 0.50 = corolla 50% open; 0.75 = corolla 75% open; 1.0 = open with petals perpendicular to the pedicel; 1.25 = flowers with petals reflexed. For heterostylous species (*Solanum lanceifolium*, *S. cordovense* and *S. nudum*), only the data from long-styled flowers are shown. Error bars around each point are \pm one standard deviation. Where no bars appear, the standard deviation is zero.

Solanum erythrorichum was an exception to these generalizations. It had flowers of 2 to 2.5 cm in diameter that opened well after sunrise, but they were long-lived, persisting for up to 80 hours (over three days) (Fig. 3A). Each of its flowers opened briefly to the fully reflexed position during late afternoon of its first day before closing for the night. Its flowers then returned to the reflexed position on the second day and occasionally on the third day as well. Old flowers could be distinguished from younger flowers by the purple petals, which darken with age.

Flower production

All the species flowered at least once during the two-month period of June and July. Two of the species flowered continuously throughout the period: *Solanum nudum* and *S. erythrorichum* (Fig. 4A). *Solanum cordovense*, *S. lanceifolium* and *S. rudepannum* all flowered in late May, paused in mid-June and began to flower again in late June or July (Fig. 4A). The two species of *Lycianthes* were very different from each other in their flowering phenology. *Lycianthes hypoleuca* flowered only during early June (and presumably in late May before monitoring had begun) (Fig. 4A). *Lycianthes gorgonea* flowered for most of June and sporadically in July and still had buds present in late July.

With relation to intensity of flower production, the most prolific bloomers of the seven species were *Lycianthes hypoleuca* and *Solanum nudum*. On average, mature individuals of these species produced around 200 or more flowers (Table 1). Despite the fact that *L. hypoleuca* possesses much larger flowers, the display produced by *S. nudum* overwhelmed that of *L. hypoleuca* because of the sheer number of individuals flowering. While only six of the *L. hypoleuca* individuals monitored flowered, all 25 *S. nudum* individuals flowered, producing a total of 4936 flowers over the 52-day monitoring period. *Solanum lanceifolium* produced the fewest flowers during the monitoring period (Table 1). Considering the number of buds present on individuals at the end of the study, *S. lanceifolium* probably produced quite a large display in August.

Regression analyses revealed significant relationships between canopy cover and flower production for several species. Individuals of both *Solanum cordovense* and *S. lanceifolium* in the shade produced significantly fewer flowers ($p=0.04$, $p=0.02$ respectively). As colonizers of disturbed areas and secondary forest, these species probably have a low tolerance for shady conditions. Increased canopy cover was also related to a greater proportion of male (short-styled) flowers in the andromonoecious *S. nudum* (Smith & Knapp, in prep.).

Fruit production

The first species to produce fruit was *Solanum rudepannum*. Its round, green berries were becoming mature in late May and were almost entirely gone by mid-June (Fig. 4B). The fruit of *S. cordovense* were the next to mature, turning from green to a deep purple-black in late June (Fig. 4B). The soft, sweet berries were consumed, probably by birds, in June and July. The fruit of *S. lanceifolium* matured in July, shortly after those of *S. cordovense* (Fig. 4B). Its scarlet berries were not nearly so sweet but quite piquant (pers. obs.). When the berries of *S. lanceifolium* were fully ripe, the fruiting vines attracted large numbers of birds (N. Bol, pers. comm.). *Solanum erythrorichum*, unlike the previous three species, had mature fruit available for the majority of the monitoring period (Fig. 4B). Starting in mid-June, its ripe green fruit began to be taken, although new fruit quickly replaced them. The fruit of the remaining three species were not yet ripe when the monitoring period concluded although it appeared that the fruit of *S. nudum* would mature

first in August, followed by *Lycianthes gorgonea* then *L. hypoleuca* (Fig. 4B).

The amount of fruit produced during June and July varied greatly among the seven species (Table 1). *Solanum nudum* produced the largest number of fruit per individual on average, closely followed by *S. rudepannum*. *Lycianthes gorgonea* produced the fewest, around 13 per individual on average, which was anticipated considering its small floral display (Table 1).

Flower visitors

Bees of the families Colletidae, Halictidae and Apidae (Michener, 2000) were the only insects observed to visit, vibrate (buzz) and presumably pollinate the flowers of *Solanum* and *Lycianthes* (listed in Table 2). Pollination is normally effected only by floral visitors that vibrate or buzz the flowers in buzz-pollinated flowers, so we have generally assumed that the visitors we observed were legitimate pollinators of these species. Flowers bagged as part of another study (Smith & Knapp, in prep.) never set fruit. Members of the three bee families we observed at LCRS comprise most of the pollinators of melittophilous Solanaceae (Linsley & Cazier, 1963; Sazima et al., 1993; Raw, 2000). The frequency of visits by the bee species to the study taxa is shown in Table 3. The bees were most active in the morning, and this activity tapered off quickly as the day progressed, a foraging pattern commonly observed in tropical bees (Knapp, 1986; Roubik, 1989). The earliest visitor by far was *Megalopta* sp., which began foraging on *L. hypoleuca* between 0415 and 0430 hours. It was also noted that larger bees tended to be most active early in the morning while smaller bees were active throughout the morning and sometimes into the afternoon (Table 2).

Most bees extracted pollen by buzzing the flower although some small bees obtained pollen by digging into the pores and scavenging on floral parts, as has been observed elsewhere (Anderson & Symon, 1988; Storti, 1988). Bees occasionally dug into the pores after first attempting to buzz the flower, a behaviour that appeared to widen the aperture, allowing the pollen to escape. Neither bees nor other insects were seen to 'rob' pollen by cutting holes into the anthers. In general, large bees visited for shorter periods of time than smaller bees (Table 2), an observation also made by Anderson & Symon (1988). In general, small bees visited small flowers (e.g., those of *Solanum nudum*) while larger bees visited the large flowers (e.g., those of *Lycianthes hypoleuca*).

All bees appeared to locate flowers visually, and were often seen approaching from afar. Once on the flower, bees positioned themselves so that their venter covered the pores of the anthers, and buzzed the anthers to extract the pollen. While buzzing, medium to small bees rotated up to 5 or 6 times to obtain the maximum amount of pollen from each anther. Large bees rotated only once or twice and sometimes not at all. The weight of the large bees was sufficient to invert the flowers, further assisting pollen extraction (Linsley & Cazier, 1963). Bees rarely visited the same flower twice (also noted by Shelly & Villalobos, 2000) and recognition of 'buzzed' flowers may have been assisted by physical changes to the flower. For example, damage by tarsal claws caused bruising on the abaxial anther surface and bees preferentially buzzed flowers free from marks. This preference was tested by bagging flowers on several plants, and allowing the other flowers to be visited and buzzed. When the bags were removed and bees had a choice of buzzed and unbuzzed flowers, only unbuzzed flowers were visited.

The bees observed during this study varied greatly in constancy, as measured by visits to non-conspecifics on a single foraging trip. *Paratetrapedia* sp. was by far the most promiscuous and was observed visiting members of the Melastomataceae, Lamiaceae,

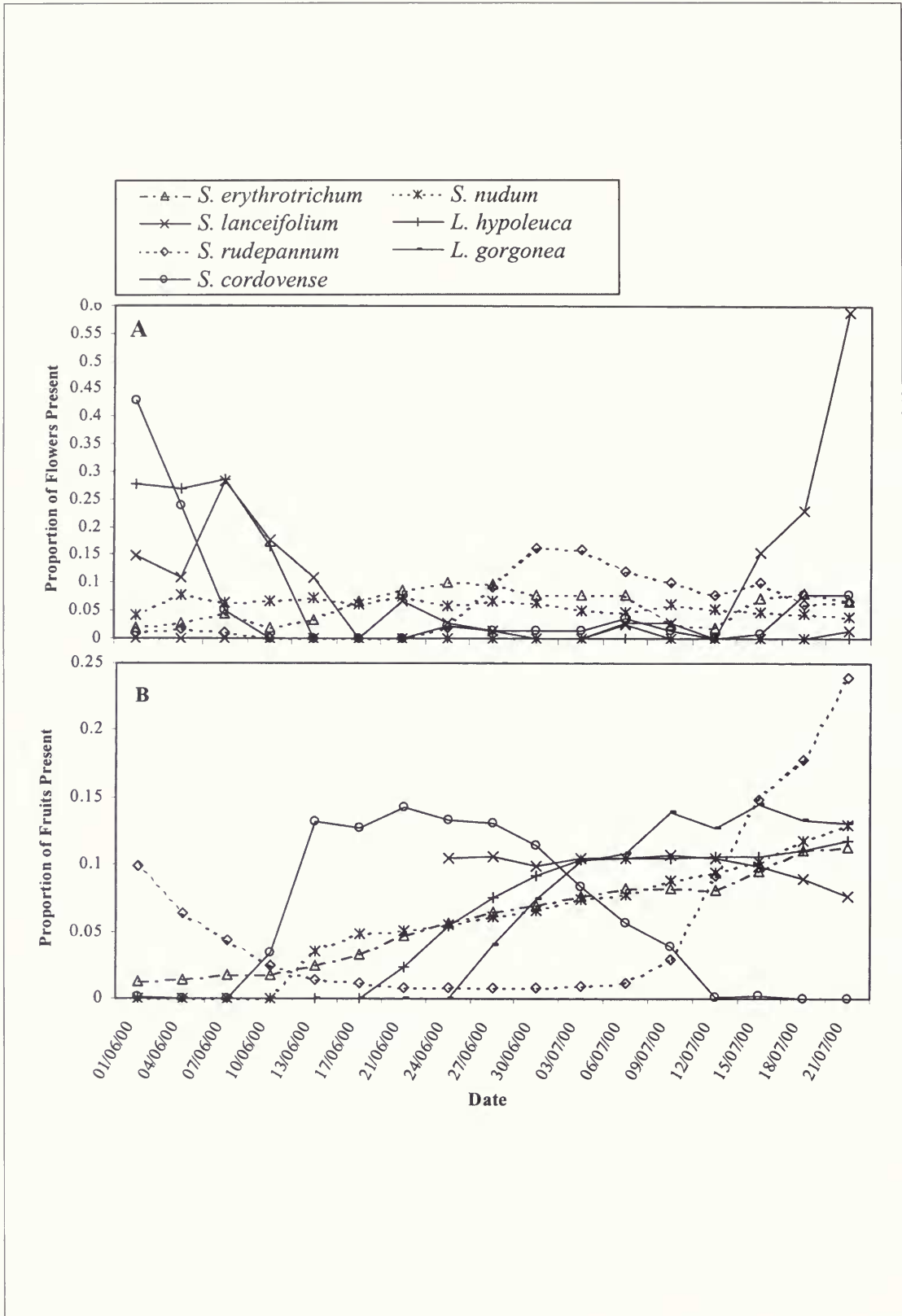


Fig. 4 Flowering (A) and fruiting (B) phenology from 1 June 2000 to 21 July 2000. Shown is the proportion of flower or fruit present on a given date. This proportion was calculated by summing the total number of flowers or fruit present on all the individuals of a species on a given date and dividing by the total number of flowers or fruit present on all the individuals of a species during the entire monitoring period. Green-fruited species have been given dashed lines; red- or black-fruited species have solid lines.

Table 1 Flowering and fruiting intensity from 1 June 2000 to 21 July 2000.

		Percentage of mature individuals monitored which flowered	Average number of flowers produced per flowering individual	Percentage of individuals monitored which fruited	Average number of fruits produced per fruiting individual
<i>S. erythrorichum</i>	(N=25)	52%	15.85	40%	13.62
<i>S. lanceifolium</i>	(N=25)	32%	4.88	60%*	22.27
<i>S. rudepannum</i>	(N=10)	50%	51.60	40%	63.50
<i>S. cordovense</i>	(N=25)	52%	16.54	44%	18.55
<i>S. nudum</i>	(N=25)	100%	197.44	80%	74.20
<i>L. hypoleuca</i>	(N=10)	60%	220.00	60%	33.83
<i>L. gorgonea</i>	(N=5)	80%	18.50	80%	12.75

* A number of individuals of *Solanum lanceifolium* were fruiting when the survey began, remained in fruit and never flowered during the study period.

Piperaceae, and Asteraceae in addition to the Solanaceae. *Paratetrapedia* sp. also flew between study species on a single foraging trip, particularly those which grew side by side, such as *Solanum rudepannum* and *S. nudum*, potentially resulting in interspecific pollen transfer. Some bees visited only solanaceous species, but were not constant to any individual species. For example, *Colletes* sp. visited *S. rudepannum*, *S. nudum* and *S. cordovense* in one foraging trip, but was never observed visiting nearby non-solanaceous species in flower. At the other end of the spectrum were bees like *Xylocopa anthophorides* and *Xylocopa* sp., which were only observed to visit a single study species (Table 2).

Pollen load analysis

Analysis of pollen loads corroborated field observations that suggested varying levels of constancy among bees. The percentage of pollen from Solanaceae varied from 69.95 to 100.00. More promiscuous pollinators such as *Paratetrapedia* sp. carried lower amounts of solanaceous pollen whereas constant pollinators like *Xylocopa* carried nearly 100% (Table 2). Overall, visitors to the seven study species carried a very high percentage of solanaceous pollen. Unfortunately, it was not possible to distinguish between the pollen of the seven study species.

The size of the pollen load found on the pollinator species generally depended on the size of the bee and how well developed its corbiculae were. Larger bees with well-developed corbiculae such as *Xylocopa* spp. and *Eulaema* sp. carried the most pollen (Table 2), followed by small- and medium-sized apid bees such as *Exomalopsis* sp. 2 and *Melipona* sp. with large corbiculae and hairy bodies (Table 2). The less hairy halictids, which lack corbiculae, carried small amounts of pollen, although *Megalopta* sp. was an exception in foraging only on newly opened, pollen-rich flowers of *Lycianthes hypoleuca*.

DISCUSSION

Floral phenology

Patterns of flower movements (i.e., opening and closing of the corolla) often relate to pollination syndrome. Most flower visitation took place in the morning hours, when fresh flowers were presented. Some individuals of *L. hypoleuca* opened their flowers before dawn, allowing pollination by the night-foraging *Megalopta* sp. (Hopkins et al., 2000). Only a few bees foraged throughout the day and these tended to visit plant species that were offering fresh flowers throughout the day, such as *S. nudum*.

Flower movements varied slightly depending on location; e.g., flowers of the individuals of *Lycianthes hypoleuca* near the Las

Cuevas field station opened around 0500 and closed between 1900 and 2100 while those near the observation tower were open between 0430 and 1500 to 1700. The light from the LCRS generator at the former site may account for this difference. Individuals in the sun occasionally had slightly different phenology from those in the shade; e.g., *S. cordovense* in the sun kept their flowers open for a greater number of consecutive days than those in the shade.

Primack (1985) compared the longevity of flowers in major habitat classes and found that most tropical forest species have one-day flowers, regardless of their pollinators. Furthermore, he suggested that within these classes, some variation in longevity within related taxa may be due to flower size. Primack postulated that large flowers would be expected to last longer than small flowers because plants expend more energy to produce them. The present study indicated that the exact opposite is true. The largest-flowered species, with the exception of *S. erythrorichum*, were the most short-lived. This suggests a trade-off between size and longevity where a plant can either maintain energetically-expensive large flowers for a short time or small energetically-inexpensive flowers for a longer time.

Flower production

Available surveys of flowering phenology in the seasonal tropics indicate that most species exhibit a definite peak or series of peaks in flowering and fruiting at some time during the year (Croat, 1969; Opler et al., 1980; Tanner, 1982; Newstrom et al., 1994). Flowering times for tropical understory herbs and shrubs, like *Solanum* and *Lycianthes*, are often clustered around the transition period from the dry to the wet season (Augspurger, 1983; Knapp, 1986; Oliviera & Gibbs, 2000). This pattern may relate to plants' resource needs such as amount of precipitation (Croat, 1969; Augspurger, 1980, 1983) or their use of environmental cues like temperature to time reproductive activities (Levin, 1978). In the present study, it was only possible to track the study species for two months, an insufficient time to draw conclusions about the phenology over the course of a year or even a season. Locating large numbers of mature individuals in the study area was problematic for the two species of *Lycianthes* and for *S. rudepannum*. Thus, the data presented here provide a preliminary picture of flower production for these seven species.

Plant guilds, i.e., sympatric species sharing a pollination syndrome, may exhibit staggering of flowering times (e.g., Heithaus et al., 1974; Newstrom et al., 1994). Although the buzz-pollinated Solanaceae at LCRS can be considered a guild (Sakai et al., 1999; Murray et al., 2000), there did not appear to be a sequence of flowering times within the study period. Knapp (1986) described a similar situation with eight species of *Solanum* section *Geminata* in Monteverde, Costa Rica, which had randomly distributed and largely overlapping flowering peaks over a year, with some species blooming more than once. Our finding that the multiple buzz-pollinated

Table 2 Pollinators of *Solanum* and *Lycianthes* species at Las Cuevas. Size classes (length from head to tip of abdomen): Small (<0.75); Medium (0.75–1.25 cm); Large (>1.25 cm).

Family	Species (number observed)	Size	Pollen baskets	Time of visits	Average length of visits per flower (seconds)	Number of individuals collected	Average density of pollen	Percent solanaceous pollen	<i>S. erythrorichum</i>	<i>S. lanceifolium</i>	<i>S. rudepannum</i>	<i>S. cordovense</i>	<i>S. nudum</i>	<i>L. hypoleuca</i>	<i>L. gorgonea</i>	Total species visited	
Colletidae	<i>Colletes</i> sp. (12)	Medium	No	1000–1320	6.9	3	2.00	100.00	✓	✓	✓	✓	✓	✓	✓	3	
	<i>Lasioglossum</i> sp. (2)	Small	No	1115	1.0	1	1.00	94.60	✓	✓	✓	✓	✓	✓	✓	2	
Halictidae	<i>Augochloropsis</i> sp. (5)	Medium	No	1020–1200	1.1	1	1.00	100.00								1	
	<i>Megalopta</i> (16)	Medium	No	0415–0535	6.3	4	4.00	99.25							✓	1	
	<i>Xylocopa anthiophorides</i> (10)	Large	Yes	0615–0700	3.0	1	1.00	98.33	✓							1	
	<i>Xylocopa</i> sp. (9)	Large	Yes	0545–0800	2.1	1	5.00	100.00							✓	1	
	<i>Xylocopa</i> cf. <i>ornata</i> (13)	Large	Yes	0615–0930	1.6	2	4.00	97.98							✓	1	
	<i>Exomalopsis</i> sp. 1 (35)	Small	Yes	0700–0900	9.3	4	3.75	99.80							✓	1	
	<i>Exomalopsis</i> sp. 2 (1)	Small	Yes	0800	4.0	1	1.00	100.00							✓	1	
	<i>Paratrapedia</i> sp. (89)	Small	Yes	0800–1640	8.7	4	1.00	72.80	✓	✓	✓	✓	✓	✓	✓	✓	6
	<i>Eufriestia</i> sp. (11)	Large	Yes	0530–1000	1.5	1	1.00	99.00	✓	✓	✓	✓	✓	✓	✓	✓	2
	<i>Euglossa</i> sp. (5)	Medium	Yes	0615–1115	1.8	1	1.00	96.70	✓	✓	✓	✓	✓	✓	✓	✓	2
	<i>Eulaema</i> sp. (8)	Large	Yes	0530–0900	1.7	1	4.00	99.00							✓	1	
	<i>Melipona fasciata</i> (12)	Medium	Yes	0630–0900	4.1	2	3.50	98.50							✓	1	
	<i>Melipona</i> sp. (132)	Medium	Yes	0530–1000	4.4	14	3.54	99.15							✓	2	
	<i>Trigona</i> sp. 1	Small	No	–	–	–	1	1.00	100.00						✓	1	
	<i>Trigona</i> sp. 2 (1)	Small	No	1135	2.0	2	1.00	69.95	✓	5	4	2	1	6	9	1	

Table 3 Frequency of pollinator visits on *Solanum* and *Lycianthes* species at Las Cuevas. For each study species, flower hours was calculated from a series of observations (1 to n) using the following equation: $O = (F_1 \times H_1) + (F_2 \times H_2) + \dots + (F_n \times H_n)$, where O equals the number of flower-hours, H equals the number of hours a given plant was observed, and F equals the number of flowers present on the plant at the time of observation.

Species	Total number of hours observed	Total number of flowers observed	Number of flower-hours observed	Pollinating visitors per flower-hour	Common pollinators (number which visited during hours observed)
<i>S. erythrorichum</i>	21.40	61	160.53	0.131	<i>Paratetrapedia</i> sp. (17)
<i>S. lanceifolium</i>	19.13	79	125.55	0.016	<i>Xylocopa anthophorides</i> (10) <i>Paratetrapedia</i> sp. (22) <i>Eufriesia</i> sp. (10) <i>Euglossa</i> sp. (4)
<i>S. rudepannum</i>	18.10	242	595.93	0.037	<i>Paratetrapedia</i> sp. (16) <i>Colletes</i> sp. (5)
<i>S. nudum</i>	49.45	1077	2175.77	0.018	<i>Paratetrapedia</i> sp. (27) <i>Colletes</i> sp. (5) <i>Augochloropsis</i> sp. (5)
<i>S. cordovense</i>	20.52	82	116.25	0.017	<i>Colletes</i> sp. (2)
<i>L. hypoleuca</i>	19.52	1190	2017.02	0.116	<i>Megalopta</i> sp. (16) <i>Xylocopa</i> sp. (9) <i>Xylocopa</i> cf. <i>ornata</i> (13) <i>Eulaema</i> sp. (8) <i>Melipona fasciata</i> (12) <i>Melipona</i> sp. (131) inconclusive
<i>L. gorgonea</i>	19.00	28	71.03	0.014	

species in the Solanaceae, which share many of the same pollinators, flower simultaneously is consistent with Feinsinger's (1987) observation that pollinator-sharing between sympatric species does not always cause temporal segregation of flower production.

Fruit production

Vertebrates are the dispersal agents for the majority of Neotropical plant species (Howe & Smallwood, 1982; Janzen, 1983; Murray et al., 2000). For species dependent on biotic dispersal agents, optimization of seed dispersal may involve staggering the time of fruit maturation to avoid interspecific competition for seed-dispersers (Levin, 1978; Fleming, 1985). Staggering of fruiting season has been recorded in the tropical forests of Trinidad in species of *Miconia* (Melastomataceae), whose fruits are dispersed by frugivorous birds (Snow, 1965). At LCRS, it appeared that time of fruit maturation in species potentially sharing the same dispersal agents was somewhat temporally separated. For instance, the brightly-coloured fruit of *Solanum cordovense* matured in late June and early July, those of *S. lanceifolium* in mid-July and those of *Lycianthes gorgonea* in August. By separating the time of fruit maturity, *Solanum* and *Lycianthes* species may maximize seed dispersal and provide a more constant supply of food for frugivorous birds and bats. However, several years of monitoring would be needed to test the staggering of fruit production and dispersal, as variability in seasonal patterns can be high (Wheelwright, 2000).

Flower visitors

Bees, particularly *Xylocopa*, *Eufriesia*, *Euglossa*, *Eulaema*, *Melipona*, *Trigona* and *Exomalopsis* species, are extremely important pollinators in neotropical forests (Endress, 1994). At La Selva, Costa Rica, for instance, Kress & Beach (1994) record that bees pollinate 38.4% of all plant species, making them the most numerically important pollinators. Our observations at LCRS revealed a diverse array of bees in the Colletidae, Halictidae and Apidae visiting *Solanum* and *Lycianthes*, including many genera observed to pollinate Solanaceae in other tropical habitats (Knapp, 1986; Storti, 1988). Large showy white-flowered species, like *S.*

lanceifolium and *L. hypoleuca*, attracted mainly medium and large bees. As the flowers of these two species usually lasted for one day only and opened around sunrise, flower visitors could depend on fresh flowers full of pollen each day and responded by returning daily to forage early in the morning. Longer-lived flowers did not draw such a loyal following. The flowers of *S. erythrorichum* and *S. nudum*, for example, attracted mostly *Paratetrapedia* sp., the small promiscuous bee. Because the flowers opened more or less at random and remained open for several days, bees could not depend on a reliable supply of fresh pollen at a certain time of day. Thus, foraging activity on these species with 'long-lived' flowers was spread throughout the morning and early afternoon.

The pollination ecology of two study species remains unclear. Very few visits were observed on individuals of *Solanum cordovense*. Although its flowers are morphologically similar to *S. nudum*, its small display failed to attract a similar suite of flower visitors. No visitors to *Lycianthes gorgonea* were observed during the study. Its few scattered individuals also produced a small display, never more than ten flowers at a time.

Pre-dawn pollination, as observed in *Lycianthes hypoleuca*, is not unknown in buzz-pollinated Solanaceae. Linsley & Cazier (1963) recorded pollination of *Solanum elaeagnifolium* Cav. and *S. rostratum* Dunal by *Ptiloglossa* and *Caupolicana* (Colletidae) up to an hour before dawn in desert habitats in Arizona. Our finding that flowers of *Lycianthes hypoleuca* open in the darkness and are pollinated before sunrise is particularly interesting because some members of the genus appear to open exclusively at night. Many white-flowered species of *Lycianthes* are nocturnal or crepuscular bloomers (Benítez & D'Arcy, 1997), and flowers are closed during the day (Nee, 1981). No studies of flower longevity or movements have been undertaken with these species however, so it is unclear whether *L. hypoleuca* is unusual in its floral phenology. Members of *Lycianthes* section *Meizodontae*, a small group of primarily Mexican herbs, have flowers that open at dawn and close during the day (Dean, pers. comm., July 2000). These flowers are pollinated by small solitary bees, and open and close over the course of several days. This diversity of floral phenologies in the genus *Lycianthes* suggests adaptive radiation to access different suites of pollinators.

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